A Reconsideration of the Taxonomic Status of Euphydryas editha koreti (Lepidoptera: Nymphalidae) from the Central Great Basin

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Abstract. Samples of Euphydryas editha lehmani and Euphydryas editha koreti from the central Great Basin and Euphydryas editha gunnisonensis from the western and central Rocky Mountains of Utah and Colorado were assayed for isozyme variability at 19 protein loci. Genetic identity estimates and the resulting phenogram show that Euphydryas editha koreti is not genetically differentiated from Euphydryas editha lehmani. These results are consistent with the spatial distribution of Euphydryas editha koreti which exists as a number of isolated alpine populations. They also suggest that Koret's checkerspot butterfly is not a cohesive evolutionarily significant unit and thus may not warrant subspecific status.

INTRODUCTION

Koret's checkerspot butterfly, Euphydryas editha koreti (Murphy and Ehrlich 1983), was described from high alpine ridges and slopes on isolated mountain ranges in the Great Basin. The subspecies is distinguished from a more widespread Great Basin subspecies, Euphydryas editha lehmani (Gunder 1929), by its much smaller size and greater yellow coloration of the submarginal band on its dorsal hindwing (Murphy and Ehrlich 1983, Austin and Murphy 1995).

In addition to that quite consistent morphological distinctiveness, Euphydryas editha koreti was acknowledged with subspecific status because of several marked ecological differences with Euphydryas editha lehmani (Murphy and Ehrlich 1983). Dramatic elevational differences exist between the habitats of the two subspecies; Euphydryas editha lehmani occurs from 1600 m to 2500 m in elevation, while Euphydryas editha koreti occurs above 3700 m. Euphydryas editha koreti apparently oviposits exclusively on Castilleja lapidicola, while Euphydryas editha lehmani oviposits on C. chromosa and Pedicularis semibarbata across most of its Great Basin distribution, and on C. linariifolia in the Pequop Mountains (Murphy and Ehrlich 1983). Finally, Euphydryas editha lehmani tends to fly in late May or early June, while the flight season for Euphydryas editha koreti is often delayed until early July, or in some years, late July. Individuals

assignable to the two subspecies have never been observed flying together.

These phenotypic and ecological differences notwithstanding, substantial doubt is cast on the appropriateness of designating populations currently assigned to *Euphydryas editha koreti* as a subspecies distinct from *Euphydryas editha lehmani*. Here, we present allozyme data that indicate that *Euphydryas editha koreti* is not particularly well differentiated genetically from *Euphydryas editha lehmani* and that populations of Koret's checkerspot butterfly do not constitute a coherent evolutionary entity with common immediate ancestry.

MATERIALS AND METHODS

Specimens of Euphydryas editha lehmani were collected from a total of seven localities in seven Great Basin mountain ranges (Toiyabe Range, Toquima Range, Monitor Range, White Pine Mountains, Egan Range, Schell Creek Range, and Snake Range), and Euphydryas editha koreti was collected from three localities; one each in the Toiyabe, Schell Creek, and the Snake Ranges (Figure 1). In addition, seven samples of Euphydryas editha gunnisonensis were collected from the Rocky Mountains of Utah and Colorado (Britten et al. 1994). This sampling regime provided the opportunity to compare genetic differences among the three Euphydryas subspecies, with the two subspecies from the Great Basin being represented by isolated but interspersed populations, and the Rocky Mountain subspecies being geographically separate from the other two (Figure 1). All samples were collected between 1980 and 1983.

Allozyme variation was assayed at 19 presumptive loci using horizontal starch-gel electrophoresis. Details of allozyme assay methods can be found in Brussard et al. (1985) and Baughman et al. (1990).

Nei's (1978) unbiased genetic identities were calculated between each pair of samples in the study. This index of genetic similarity based on allele frequencies provides a metric that can be used to derive a phenogram that is a graphical representation of the genetic similarities among the assayed populations. The UPGMA clustering algorithm was used in this analysis. BIOSYS-1 (Swofford and Selander 1981) was used for all data analyses.

RESULTS

Total sample sizes were 143 for Euphydryas editha koreti, 282 for Euphydryas editha lehmani, and 438 for Euphydryas editha gunnisonensis. Unbiased genetic identities (Nei 1978) among the 17 Euphydryas editha populations sampled are given in Table 1. Mean observed population heterozygosities were nearly identical among the three subspecies; 0.057±0.009, 0.058±0.022, and 0.061±0.023 for Euphydryas editha koreti, Euphydryas editha lehmani, and Euphydryas editha gunnisonensis, respectively. Genetic identities of 1.00 were estimated among three of the four Gunnison Basin populations (AL, AS, and JC) and between NS, an Euphydryas editha koreti sample from the Schell Creek Range, and ANT, an Euphydryas editha lehmani

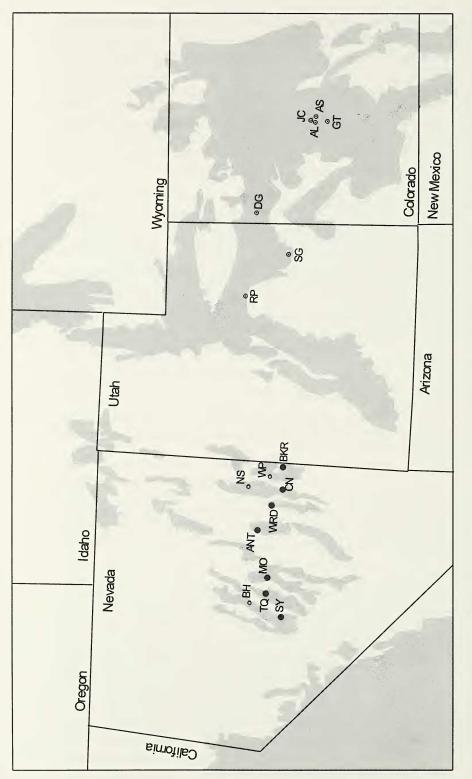


Figure 1. Map of Euphydryas editha collection sites with subspecies Euphydryas editha koreti (open circles), Euphydryas editha lehmani (closed circles), and Euphydryas editha gunnisonensis (dotted circles) indicated. Shading represents areas over 2,200 meters elevation.

Table 1. Pairwise estimates of unbiased genetic identity (Nei 1978) for 17 samples of Euphydryas editha. Subspecies lehmani and koreti were sampled from Nevada and subspecies gunnisonensis was sampled from Utah and Colorado.

Population			2	က	4	2	9	7	œ	6	10	Ξ	12	13	4	15 1	16
1 SY lehmani	*	* * * * *															
2 BH koreti	0	0.994															
3 TQ lehmani	0	0.983 0.984	0.984														
4 MO lehmani	0	0.992	0.993	0.993													
5 ANT lehmani	0	.992	0.992 0.992		0.991 0.997												
6 WRD lehmani	0	994	0.994 0.993	0.995	0.999	0.997											
7 NS koreti	0	.993	0.993 0.991	0.994	0.998		1.000 0.999										
8 CN lehmani	0	166	0.991 0.991	0.997	0.998	966.0	0.999	0.998									
9 WP koreti	0	986	0.987	0.993	966.0	0.999	0.995	0.998	0.995								
10 BKR lehmani	0	786.	0.986	0.986	0.993		0.996 0.992	0.996	0.991	0.991 0.996							
11 RP gunnisonensis		.951	0.947	0.956	0.960	0.973	0.959	0.970	0.958	0.978	0.977						
12 SG gunnisonensis		.962	0.958	0.968	0.969	0.982	0.969	0.979	0.968	0.987	0.983	966.0					
13 DG gunnisonensis		926	0.955	0.963	0.964	0.979	0.963	0.974		0.963 0.983	0.979	0.994	0.998				
14 GT gunnisonensis		1967	0.967	0.973	976.0	0.987	0.975	0.983		0.973 0.990	0.986	0.600		0.995 0.997			
		.947	0.947	0.957	0.959	0.974	0.956	0.968	0.956	0.956 0.979	0.975	0.992		0.996 0.999	0.997		
16 JC gunnisonensis		1.957	0.957 0.957 0	996.0	0.969	0.982	0.967	0.967 0.976	996.0	0.966 0.986	0.982	0.982 0.993		0.997 0.999	0.999 1.000	1.000	
17 AL gunnisonensis		.955	0.954	0.963	0.965	0.979	0.963	0.963 0.965 0.979 0.963 0.974 0.962 0.983	0.962	0.983	0.980	0.980 0.994	0.997	0.997 0.999		0.999 1.000 1.000	000

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sample from the White Pine Mountains (Table 1). The lowest estimates of genetic identity (I=0.95) were found between Euphydryas editha gunnisonensis populations from the central Rocky Mountains and Euphydryas editha lehmani and Euphydryas editha koreti samples from the Toiyabe Range. The UPGMA phenogram derived from genetic identity estimates separates Euphydryas editha gunnisonensis from the other two subspecies included in the study, while Euphydryas editha koreti samples are imbedded among Euphydryas editha lehmani samples (Figure 2). Euphydryas editha gunnisonensis is separated from the other subspecies at a mean genetic identity of about 0.97 (Figure 2).

DISCUSSION

Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." It has long been recognized, therefore, that the subspecies category does not necessarily reflect patterns of differentiation that have evolutionary significance; hence the category should be used only to delineate groupings of populations that share phenotypic similarity (Wilson and Brown 1953). Debate has continued since the 1950's over the taxonomic importance of the subspecies category and how the category should be defined (Ehrlich 1957, Lidicker 1962, Mayr 1982, Cracraft 1989). The purpose here is not to revisit that debate, but to point to the general agreement that the possession of a trinomial appellation by a group of populations does not necessarily mean that those populations constitute an evolutionarily significant unit (Mayr 1982, Cracraft 1989). The subspecies category should be used simply as a convenience for delineating groups of geographically proximate, morphologically similar forms discernable from other such groups (Mayr 1982). In that light, the interspersed distribution of Euphydryas editha lehmani and Euphydryas editha koreti presents a taxonomic problem.

The suite of alpine populations of *Euphydryas editha* found in the Schell Creek, Snake, and Toiyabe Ranges of Nevada was described as the subspecies *Euphydryas editha koreti* Murphy and Ehrlich based on ecological and morphological differences of these individuals when compared to specimens of the more widespread montane subspecies found at lower elevations, *Euphydryas editha lehmani*. Although all *Euphydryas editha koreti* populations are found in nearly identical ecological situations, they are completely isolated from one another and are at least partially surrounded by *Euphydryas editha lehmani* populations at lower elevations (Figure 1). Because of those discontinuities in the distribution of *Euphydryas editha koreti* (Figure 1), this subspecies is described as "polytopic," that is, it shows "independent recurrence of similar or phenotypically indistinguishable populations in geographically separated areas" (Mayr 1969). For many workers this current

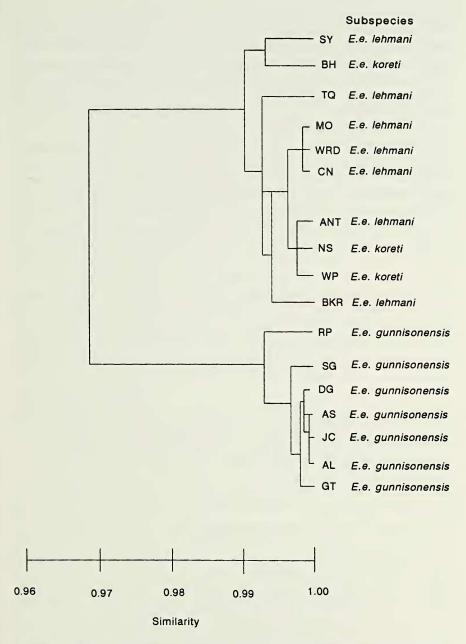


Figure 2. UPGMA phenogram based on Nei's (1978) unbiased genetic identities for 17 sampled populations of *Euphydryas editha*. Three subspecies are represented: *Euphydryas editha lehmani* and *Euphydryas editha koreti* from Nevada, and *Euphydryas editha gunnisonensis* from Utah and Colorado. Cophenetic correlation coefficient is 0.885. Note that the relationships involving the BKR and AS populations are incompletely resolved on the phenogram.

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spatial distribution, this polytopy, disqualifies *Euphydryas editha koreti* from subspecies status (e.g. Wilson and Brown 1953, Mayr 1963 and 1969). If, however, populations referred to as *Euphydryas editha koreti* were to show high levels of genetic similarity to one another when compared to geographically adjacent populations of the same species, common ancestry could be inferred for *Euphydryas editha koreti* populations. This would suggest a more continuous distribution in the past, and perhaps defensible subspecific status.

The allozyme results presented do not show such coherence, and they provide little support for the subspecific status of Euphydryas editha koreti. This conclusion is based on the UPGMA phenogram in Figure 2 and the geographic distribution of Euphydryas editha koreti. Previous work by Brussard et al. (1985), using nearly identical methods, provided a framework from which taxonomic decisions can be made using allozyme data at taxonomic levels below the subfamily. The mean genetic identity among 12 subspecies in the tribe Melitaeini, including several Euphydryas editha subspecies, was 0.964 (Brussard et al. 1985). This estimate of mean identity is nearly equal to the genetic identity observed between the Euphydryas editha gunnisonensis and Euphydryas editha lehmani - Euphydryas editha koreti clusters in Figure 2. This result suggests that at least some "good" subspecies exist among montane Euphydryas editha populations in the central Great Basin and Rocky Mountain regions.

The clustering of Euphydryas editha koreti with Euphydryas editha lehmani, however, indicates much greater genetic similarity among these populations and supports the conclusion that Euphydryas editha koreti is probably not an evolutionarily significant unit, but is instead a recurrent high elevation phenotype of Euphydryas editha lehmani. While it is impossible to dismiss a scenario in which low elevation populations were established from ancestral high elevation populations, and subsequently became the most widespread phenotype in the Great Basin; the most likely biogeographic scenario is that different low elevation populations have given rise independently to alpine populations sharing convergent phenotypes in the three Great Basin mountain ranges where Euphydryas editha koreti is known to occur. The tight clustering of the Toivabe Range samples, one of Euphydryas editha lehmani (SY, Figure 1) and the other Euphydryas editha koreti (BH, Figure 1), in the phenogram (Figure 2) provides the best evidence of a high degree of similarity between these two taxa. The allozyme data suggest that, despite the phenotypic similarity of individuals from populations assigned to Euphydryas editha koreti and their distinctiveness from individuals from geographically adjacent areas, they should not be recognized as taxonomically distinct from the more widespread Euphydryas editha lehmani. Furthermore, the data also suggest that Euphydryas editha koreti are not evolutionarily distinct from nearby Euphydryas editha lehmani populations at lower elevations.

The Euphydryas editha koreti situation underscores the lack of formal nomenclatural tools available to describe phenotypically distinct entities that do not fit the subspecies category. This difficulty is expected to be particularly acute for well studied taxa, such as Lepidoptera, for which there is a long standing tradition of "splitting." Current nomenclatural precedence would call for the "sinking" of Euphydryas editha koreti into the subspecies Euphydryas editha lehmani. This approach. however, would leave a morphologically distinct form, now referred to as Euphydryas editha koreti, without the unique designation. Another approach would be to recognize an additional taxonomic category for polytopic subspecies. This approach is neither particularly parsimonious nor traditional, is likely to be cumbersome, and its application would surely meet resistance. It is clear that this sort of taxonomic dilemma will only increase in frequency as molecular genetic techniques become more widely available and the taxonomic status of an increasingly broad spectrum of organisms comes under scrutiny.

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